

ON THE SPECIES AND POPULATIONS OF THE
GENUS *ACANTHOCEPHALUS* (ACANTHOCEPHALA:
ECHINORHYNCHIDAE) FROM NORTH AMERICAN
FRESHWATER FISHES: A CLADISTIC ANALYSIS

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Abstract.—Cladistic analysis provided greater understanding and further support of the evolutionary relationships among the species and populations of the genus *Acanthocephalus* from North American freshwater fishes outlined earlier by Amin (1985). It is proposed that *A. dirus*, *A. tahlequahensis* and *A. alabamensis* are monophyletic with *A. dirus* representing a probable successful and persistent general ancestor. The two southern species are more closely related to each other than either one is to *A. dirus*, probably evolved allopatrically, and now exhibit new restricted distributions. Within *A. dirus*, the Mississippi River and Wisconsin-Lake Michigan populations are more closely related to each other than either one is to the New England population, which may have been evolving in isolation longer than the former two.

The recent revision of the genus *Acanthocephalus* from North American freshwater fishes by Amin (1984) and Amin and Huffman (1984) established the presence of three species, *A. dirus* (Van Cleave 1931), *A. tahlequahensis* Oetinger and Buckner, 1976, and *A. alabamensis* Amin and Williams, 1983. *Acanthocephalus dirus* has the widest host and geographical distribution and exhibits the greatest morphological variability. It is found in 65 species and 16 families of fish mostly in the Mississippi River drainage system (or waters previously connected to it in Ohio and Lake Erie) in 13 states in the U.S. (Amin 1985). *Acanthocephalus tahlequahensis* is found in four species and two families of fish from Oklahoma and *A. alabamensis* in six species and four families from Alabama.

Three distinct populations are recognized within *A. dirus* by Amin (1984): the Mississippi River population; the Wisconsin-Lake Michigan population (= *A. parksidei* Amin, 1975) and the New England population (= *A. jacksoni* Bullock, 1962). The Mississippi River population has the widest

geographical (in 10 states) and host (46 fish species in 11 families) distribution and is more variable morphologically than the Wisconsin-Lake Michigan population (in two states and 22 species and 10 families of fish) or the New England population (in two states and 14 species and nine families).

Meristogram patterns (unpublished) were distinctly different in each of the three species. Within *A. dirus*, the meristogram patterns were similar in all the populations studied by Amin (1984) except the Gleason population from Kentucky which showed some elements of uniqueness corresponding with certain peculiarities discussed by Amin (1984).

Based on geological evidence as well as on variability, host and geographical distribution, Amin (1985:214) proposed that "early *A. dirus* ancestors were probably found in the Mississippi River basin before the Wisconsin glaciation." The establishment of the geographically isolated Wisconsin-Lake Michigan population "must have taken place with Mississippi River elements from the Des Plaines-Illinois River system

Table 1.—Character distribution among species of genus *Acanthocephalus* from North American freshwater fishes and outgroups.

Character distribution	Outgroups (Europe)		North American species of <i>Acanthocephalus</i>		
	X ₁ <i>A. lucii</i> ¹	X ₂ <i>A. anguillae</i> ¹	I <i>A. dirus</i>	II <i>A. alabamensis</i>	III <i>A. tahlequahensis</i>
(1) Mean male body length (mm)	Large (>5)	Large (>5)	Moderate (3–4)	Small (<3)	Small (<3)
(2) Mean female body length (mm)	Large (>10)	Large (>10)	Moderate (7–9)	Small (<6)	Small (<6)
(3) Body shape	Cylindrical	Cylindrical	Cylindrical	Cylindrical	Spindle
(4) Mean anterior testis length (μm)	Large (>800)	Large (>800)	Moderate (450–800)	Small (<450)	Small (<450)
(5) Mean anterior testis length/body (%)	Small (<15)	Small (<15)	Large (>19)	Large (>19)	Small (<15)
(6) Mean anterior testis width/body width (%)	Large (>50)	Moderate (42–46)	Large (>50)	Large (>50)	Small (<42)
(7) Mean no. proboscis hooks/row (males)	Small (<9)	Small (<9)	Moderate (9–10)	Small (<9)	Large (>11)
(8) Mean no. proboscis hooks/row (females)	Small (<9)	Small (<9)	Moderate (9–11)	Moderate (9–11)	Large (>11)
(9) Mean length of largest proboscis hooks (males) (μm)	Large (>60)	Large (>60)	Moderate (50–60)	Small (<50)	Small (<50)
(10) Mean length of largest proboscis hooks (females) (μm)	Large (>70)	Large (>70)	Moderate (60–70)	Small (<60)	Small (<60)
(11) Meristogram patterns	A ²	B ²	C	D	E

¹ From Petrochenko (1956).
² Presumably.

(tributaries of the Mississippi River . . .” in post-glacial streams like the Pike River “... after the withdrawal of the Lake Michigan lobe of the Wisconsinan ice sheet from the area between 15,000 and 12,000 years B.P.” (before the present). Based on morphological evidence alone, the geographically isolated New England population appears to have also originated from a Mississippi River *A. dirus*-like source (Amin 1985). *Acanthocephalus tahlequahensis* has a limited distribution in an Oklahoma tributary of the Mississippi River and *A. alabamensis* is found in the Mobile Bay drainage system which had continuous fauna with the Mississippi River before barriers to recent dispersal arose. The two southern species are found more typically in certain species of *Etheostoma* not parasitized by other species of *Acanthocephalus*.

The above information provides a brief background of the inter- and intraspecific associations within the genus *Acanthocephalus* from North American freshwater fishes which lends itself to further analysis within a cladistic context. To date, cladistic analysis has not been used as an aid to the understanding of acanthocephalan evolutionary biology. This method, however, was found amenable to this study as it provided greater understanding of and further support for the evolutionary relationships briefly outlined above.

Materials and Methods

Methods in Brooks et al. (1985) and Wiley (1981) as well as suggestions by Drs. D. R. Brooks and J. N. Caira were instrumental in the understanding of the findings pre-

Table 2.—Character distribution among populations of *Acanthocephalus dirus* and outgroups.

Character distribution	Outgroups			<i>Acanthocephalus dirus</i> populations		
	X ₁ <i>A. alabamensis</i>	X ₂ <i>A. tahlequahensis</i>	X ₃ <i>A. lucii</i>	I Mississippi River	II Wisconsin-Lake Michigan	III New England
(1) Mean male body length (mm)	Small (<3)	Small (<3)	Large (>5)	Moderate (3–4)	Moderate (3–4)	Moderate (3–4)
(2) Mean female body length (mm)	Small (<6)	Small (<6)	Large (>10)	Moderate (7–9)	Moderate (7–9)	Moderate (7–9)
(3) Body shape	Cylindrical	Spindle	Cylindrical	Cylindrical	Cylindrical	Robust anteriorly
(4) Mean anterior testis length (μm)	Small (<450)	Small (<450)	Large (>800)	Moderate (450–800)	Moderate (450–800)	Moderate (450–800)
(5) Mean anterior testis length/body length (%)	Large (>19)	Small (<15)	Small (<15)	Large (>19)	Large (>19)	Moderate (17–18)
(6) Mean anterior testis width/body width (%)	Large (>50)	Small (<42)	Large (>50)	Large (>50)	Large (>50)	Moderate (42–46)
(7) Mean no. proboscis hooks/row (males)	Small (<9)	Large (>11)	Small (<9)	Moderate (9–10)	Moderate (9–10)	Small (<9)
(8) Mean no. proboscis hooks/row (females)	Moderate (9–11)	Large (>11)	Small (<9)	Moderate (9–11)	Moderate (9–11)	Small (<9)
(9) Mean length of largest proboscis hooks (males) (μm)	Small (<50)	Small (<50)	Large (>60)	Moderate (50–60)	Moderate (50–60)	Large (>60)
(10) Mean length of largest proboscis hooks (females) (μm)	Small (<60)	Small (<60)	Large (>70)	Moderate (60–70)	Moderate (60–70)	Large (>70)
(11) Meristogram pattern	A	B	C ²	D	D	D

¹ From Petrochenko (1956).² Presumably.

sented in a cladistic context and in the construction and interpretation of cladograms.

Results and Discussion

Cladograms were made with the assumption that the three North American species are each others' closest relatives, and that none has closer relatives on other continents (see following parts). Adequate data were available for four species of *Acanthocephalus*: *A. lucii* (Muller, 1776), *A. anguillae* (Muller, 1780), *A. clavula* (Dujardin, 1845), and *A. falcatus* (Frolich, 1789) for use as outgroups. Resolving all characters used in the analysis (Table 1) was possible by using the first two species, i.e., their plesiomorphic states satisfactorily polarized ingroup

characters. These plesiomorphic states included large and cylindrical bodies, large testes, larger and fewer proboscis hooks per row. The choice of those characters was based on characteristics of body, testes, and proboscis hooks, the evolutionary significance of which was discussed by Amin (1984). Note that in the absence of other data (Tables 1, 2) a linear transformation series is to be preferred (Mickevich 1982). The data matrix is shown in Table 3. The resulting cladogram (Fig. 1) has a high overall consistency index (minimum number of steps/actual number of steps; see Farris et al. 1970a, b) of 95% and synapomorphic consistency of 100% indicating a low degree of parallel evolution in the characters used

and giving a high degree of confidence in the pattern hypothesized. Two other cladograms with lower consistency values were excluded from consideration. The hypothesized pattern (Fig. 1) indicates that (1) the three North American species (ingroup) are monophyletic. X_1 and X_2 plus the three North American species are postulated to form a monophyletic group based on their shared possession of a suite of four derived traits (3, 5, 6, 7 in Fig. 1). Using the two "X" species as outgroups, I, II and III are postulated to be a monophyletic group based on traits 1, 2, 4, 8, 9, 10 in Fig. 1. The hypothesis of monophyly is supported by the very high goodness of fit statistics. (2) *A. alabamensis* and *A. tahlequahensis* are more closely related to each other than either one is to *A. dirus*. The two branching points on the cladogram indicate a north-south split (*A. dirus* and the ancestor of *A. alabamensis* and *A. tahlequahensis*). Prior to its differentiation into distinct populations, *A. dirus* was of the same age as the common ancestor of the two southern species.

The most reasonable events are a widespread ancestor divided into a southern population giving rise to *A. alabamensis* and *A. tahlequahensis* and a more northern population forming *A. dirus*. Under the above conditions of monophyly, speciation would be allopatric. Figure 1 and Wiley's (1981) identical diagram (Fig. 2-10b) indicate allopatric speciation. While the identification of the persistent ancestral *A. dirus* population is possible, it is not easily detectable given available data above. It is proposed, however, that based on its broad geographical and host distributions and its great morphological variability, *Acanthocephalus dirus* appears to be a successful persistent general ancestor while *A. tahlequahensis* and *A. alabamensis* seem to exhibit new restricted distributions. *Acanthocephalus dirus* may also be interpreted as a successful adaptable new species with the other two species exhibiting relictual distributions. Some combinations of the two interpreta-

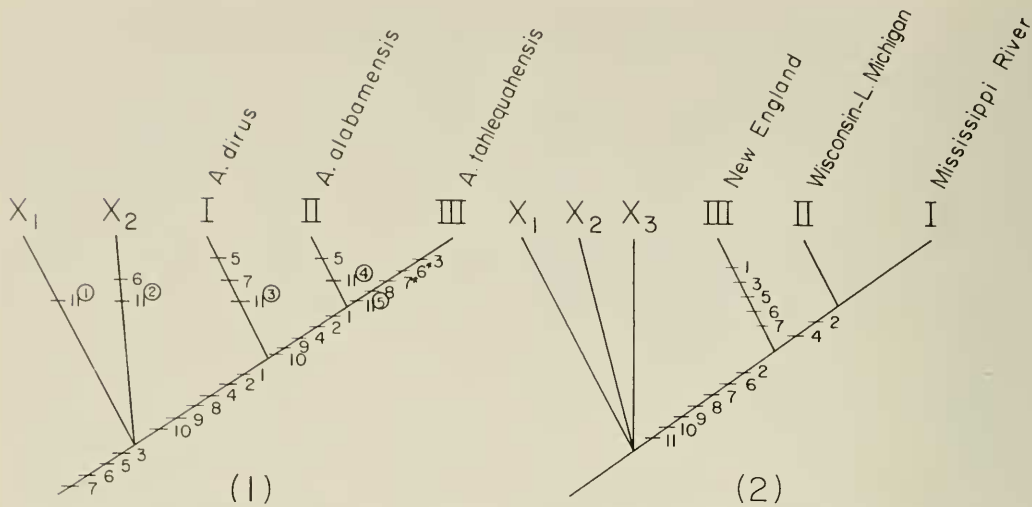
Table 3.—Data matrix of six taxa and 11 characters based on Table 1.

Character state	Taxon				
	X_1	X_2	I	II	III
1	0	0	1	2	2
2	0	0	1	2	2
3	0	0	0	0	1
4	0	0	1	2	2
5	0	0	1	1	0
6	0	1	0	0	1
7	0	0	1	0	1
8	0	0	1	1	2
9	0	0	1	2	2
10	0	0	1	2	2
11	1	2	3	4	5

tions may also be theorized. The first interpretation is, however, preferred because of the ancestral position of *A. dirus* on the phylogenetic tree (Fig. 1). This is concordant with the contention that the anatomical diversity and the broad host and geographical distributions of this species do represent generalized persistent ancestral traits and that distinguishing states of the restricted *A. alabamensis* and *A. tahlequahensis*, e.g., small size, are more recently derived.

The evolutionary relationships among the three *A. dirus* populations are expressed in cladogram Fig. 2 based on data summarized in Tables 2 and 4. This cladogram has an overall and synapomorphic consistency index of 100%. It suggests that (1) the Mississippi River and the Wisconsin-Lake Michigan populations are more closely related to each other than either one is to the New England populations, (2) the latter population may have been evolving in isolation longer than the former two if equal rates of evolution of all characters are assumed. Of the three extant populations, the New England population is the most highly differentiated, and (3) the present Mississippi River population and that of Wisconsin-Lake Michigan are equally derived.

The above interpretation of cladogram



Figs. 1, 2. Cladograms showing the phylogenetic relationships among the three North American species of *Acanthocephalus* from freshwater fishes (Fig. 1, from Tables 1 and 3) and among the three populations of *A. dirus* (Fig. 2, from Tables 2 and 4). For asterisks see Tables 1 and 3. Circled numbers (A–E, Table 1 and A–D, Table 2) indicate specific meristogram patterns different in each species.

Fig. 2 provides additional evidence to those based on geological and morphological grounds (Amin 1985) supporting the proposition that the Wisconsin-Lake Michigan population of *A. dirus* dispersed from an early Mississippi River-based source and then became geographically isolated less than 15,000 years ago. Given sufficient time and continued isolation, this situation would be a classical example of Van Cleave's (1952) earlier proposition that in Palaeacanthocephala, isolation might allow the normal extremes in a highly variable species to become segregated as distinct species. The interpretation also provides further insights into those based on morphological and clinal variations suggesting a similar process for the New England population even though the origin of its source remains to be identified. Cladogram Fig. 2 indicates that this highly differentiated population may have been evolving in isolation longer than the other two.

At the present time, it is not known whether the dispersal of *A. dirus* led to the isolation of *A. alabamensis* and *A. tahle-*

quahensis due to competitive exclusion, or that some geological or host related changes which isolated the latter two species also allowed the dispersal of *A. dirus* after the fact. It is, however, clear that certain geological events affected other aspects of the distribution and evolution of these acanthocephalans, e.g., the geographically isolated northern populations of *A. dirus*, mak-

Table 4.—Data matrix of six taxa and 11 characters based on Table 2.

Character state	Taxon					
	X ₁	X ₂	X ₃	I	II	III
1	0	0	1	2	2	2
2	0	0	1	2	2	2
3	0	1	0	0	0	2
4	0	0	1	2	2	2
5	0	1	1	0	0	2
6	0	1	0	0	0	2
7	0	1	0	2	2	0
8	0	1	2	0	0	2
9	0	0	1	2	2	1
10	0	0	1	2	2	1
11	1	2	3	4	4	4

ing the proposed geological scenario the best hypothesis presently possible.

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Literature Cited

- Amin, O. M. 1984. Variability and redescription of *Acanthocephalus dirus* (Acanthocephala: Echinorhynchidae) from freshwater fishes in North America.—Proceedings of the Helminthological Society of Washington 51:225–237.
- . 1985. Hosts and geographic distribution of *Acanthocephalus* (Acanthocephalus: Echinorhynchidae) from North American freshwater fishes, with a discussion of species relationships.—Proceedings of the Helminthological Society of Washington 52:210–220.
- , and D. G. Huffman. 1984. Interspecific variability in genus *Acanthocephalus* (Acanthocephalus: Echinorhynchidae) from North American freshwater fish, with a key to species.—Proceedings of the Helminthological Society of Washington 51:238–240.
- Brooks, D. R., J. N. Caira, T. R. Platt, and M. H. Pritchard. 1984. Principles and methods of phylogenetic systematics: A cladistics workbook. The University of Kansas Museum of Natural History Special Publication No. 12, v + 92 pp.
- Farris, J. S., A. G. Kluge, and M. J. Eckardt. 1970a. A numerical approach to phylogenetic systematics.—Systematic Zoology 19:172–189.
- , ———, and ———. 1970b. On predictivity and efficiency.—Systematic Zoology 19:363–372.
- Mickevich, M. F. 1982. Transformation series analysis.—Systematic Zoology 31:461–478.
- Petrochenko, V. I. 1956. Acanthocephala in domestic and wild animals. Akademia NAUK, Moscow, 435 pp.
- Wiley, E. O. 1981. Phylogenetics. The theory and practice of phylogenetic systematics. Wiley-Interscience Publications, New York, 439 pp.

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